

NO NEED TO COMPROMISE BETWEEN FOOD AND SAFETY FOR VINOUS-THROATED PARROTBILLS¹

LUCIA LIU SEVERINGHAUS

*Institute of Zoology, Academia Sinica,
Nankai, Taipei, Taiwan 11529,
Republic of China*

(Accepted January 11, 1991)

Lucia Liu Severinghaus (1991) No need to compromise between food and safety for vinous-throated parrotbills. *Bull. Inst. Zool., Academia Sinica* 30(3): 183-200. The habitat use pattern of birds may reflect optimal foraging, predator avoidance, or other survival pressures. The same may apply to flocking birds. They may 1) favor areas where the resources are abundant, 2) prefer areas where there is good protection against predators, or 3) prefer areas where movement is energetically least costly.

In 1983-84 I followed the activity of vinous-throated parrotbills (*Paradoxornis webbiana*) and recorded the changing quantity of their major plant foods. In 1988-89 in a 3.85 ha study area divided into 10 meter square quadrates, the activities of a parrotbill flock were monitored in conjunction with the distribution and abundance of plant foods, the vegetation profile, and the vegetation structure in each grid.

The results showed that some areas were visited daily by parrotbills, while other areas were visited every 2, 3, 4, 5 or more days. Most areas were not revisited within 5 days. Among areas revisited within 5 days, the more frequently an area was used, the more intensely it was foraged each time. Thus, some places were favored over others. Multivariate analyses show that food quantity was the primary factor influencing where the bird flock went and how long they stayed. Parrotbills also favored areas where the interbranch distance on shrubs was between 6 and 7 cm which could be covered by an easy hop. Thus, energy seems to be the primary concern for flocking parrotbills. The total number of stems in the undergrowth in a grid also contributed significantly to the variation in habitat use. Stems provided predator protection, the substrate for insect gleaning, and often carried large amounts of plant food. Apparently parrotbills did not need to bypass the better feeding locations for safety. This species probably evolved in an energy restricted situation, and their ability to conserve energy probably permitted them to have the widest distribution on Taiwan, with probably the widest niche.

Key words: Habitat use, Foraging, Predation pressure, Flocking, Energetics, Parrotbill, *Paradoxornis webbiana*.

A heterogeneous habitat is usually unevenly used by a given species of animals (Krebs, 1974). According to opti-

mal foraging theory, animals forage in areas that yield maximum return in energy (Krebs, 1978). Maximizing energy return can be accomplished by either

1. Paper No. 353 of the Journal Series of the Institute of Zoology, Academia Sinica.

increasing energy intake or decreasing energy expenditure, or a combination of the two. Charnov's model (1976) suggests that the duration an animal stays in an area is determined by the available resource patch. However, in the real world the situation is probably a lot more complex because predation pressure may cause an organism to compromise between feeding efficiency and safety (Krebs, 1978), and the habitat use pattern of a species could be influenced by a number of factors.

Animal flocking theories suggest that birds form flocks to increase the individuals' efficiency in either feeding or predator detection or both (Morse, 1967, 1970; Pulliam, 1973; Powell, 1974; Rubenstein *et al.*, 1977; Caraco, 1979; Sullivan, 1984; Berner and Grubb, 1985). Members of a flock can improve feeding efficiency by avoiding locations where the food resources have already been depleted by others (Morse, 1967; Cody, 1971; Baker *et al.*, 1981). So the habitat use pattern in flocking birds should reflect local food abundance or replenishing rates. Whelan (1989) found that different birds preferred foraging on certain types of vegetation structures. Norberg (1983) found a relationship between the spacing of trees and the foraging modes of some birds. Local vegetation structure or other habitat features may influence the amount of energy spent during foraging. Thus, birds may avoid foraging in certain areas because the vegetation structure is unsuitable.

If birds flock to decrease the danger of predation, their habitat use pattern may reflect the type and degree of predation. Yellow-eyed juncos (*Junco phaeonotus*) and house sparrows (*Passer domesticus*) preferred feeding near cover when there was a choice (Caraco *et al.*, 1980; Grubb and Greenwald 1982). This was a compromise between safety and food. Of course, birds may flock to benefit both in

feeding efficiency and predator detection by sharing vigilance, thus decreasing the time each individual spends on vigilance and increasing the time available for foraging (Powell, 1974; Barnard, 1980; Wickler, 1985). Caraco (1980) suggested that the amount of time individuals spent on surveillance and foraging should be negatively related to flock size.

The omnivorous vinous-throated parrotbill (*Paradoxornis webbiana*) is an excellent subject to investigate whether the habitat use pattern of flocking birds reflect primarily foraging concerns, or whether it indicates adaptations to other survival pressures. This species forms relatively stable single species flocks of up to 75 birds during the non-breeding season. It demonstrates almost no intra- or inter-flock aggression, and has no social hierarchy within the flock (Severinghaus, 1987). These characteristics makes a flock of parrotbills an assembly of relatively equal individuals, without the complication of aggression, dominance, or variations in food preferences found in many other single or mixed species bird flocks. This species has probably the widest niche among Taiwan birds. It inhabits types except virgin forests from sea level to 3,500 m in elevation and feeds on all types of food small enough to be handled. Perhaps because of their small size (mean weight 10.5 g), they spend most of the time during the nonbreeding season on foraging related activities (Severinghaus, 1987).

This study aims to analyze whether the habitat use pattern of parrotbills suggests optimal foraging, or shows the influence of predation or other pressures. The factors considered include food availability, the availability of substrate for gleaning insects, the type and amount of cover provided by local vegetation, and vegetation structure as it relates to travelling costs.

METHODS

This study is a part of an on-going study that began in 1983. This report covers the work conducted from 1 July 1983 to 30 June 1984, and from 15 December 1988 to 31 March 1989 on Tunghai University campus in central Taiwan (latitude: 24°10'30", longitude: 120°36'00", elevation: 220 m). When analyzing what factors might influence the parrotbill's habitat use, only data obtained during the 1988-1989 winter season were considered in order to eliminate complications caused by breeding related activities. During 1983-1984, the study site was a 35 ha area covering *Acacia confusa* woods, old fields, pastures, buildings, gardens and stream banks. Six flocks of vinous-throated parrotbills shared the area.

During 1988-1989, the study site was a 3.85 ha patch of acacia woods with a small number of *Cassia siamea* mixed in. The understory was composed primarily of *Clerodendron cyrtophyllum*, *Lantana camara*, *Panicum* spp., *Miscanthus floridulus*, *Bridelia monoica* and *Polygonum chinense*. This was the activity area of one flock of 25 parrotbills. In this habitat, the composition of the avian community was fairly simple, and the vinous-throated parrotbill was the most important species because of its large population size. Thus, there were no complications caused by competitors. November to March are the winter months with mean monthly temperatures generally in the teens and usually with low precipitation.

All together, four field assistants and several undergraduate students assisted me with data collection. Between July 1983 and March 1984, we spent every other week on the study site. We recorded the activity patterns of parrotbills in their habitat by following each bird flock, taking a census every 10 min from dawn to dusk, noting the number of birds in the focal flock, and the proportion of

birds in the flock that were active in the canopy, middle, or shrub and ground layer at the time. The number of birds active in each vegetation layer was later summed as total bird-minutes in each layer. We recorded the movement of the flocks on maps and also tracked the flowering and seedings of plants in the habitat.

In November 1988 we set up a 10 m × 10 m quadrat system in the woods (Fig. 1). Beginning in December 1988, we spent one day every other week sampling the quantity of plant foods, and the four subsequent days monitoring the activities of the parrotbill flock. About 85% of the vinous-throated parrotbills have been previously caught and color marked for individual identification. During this study period, as we followed the bird flock, we recorded the time, the exact location, the number of birds in the flock, their behavior and which stratum (strata) of the habitat they were using.

Between 1983 and 1988, parrotbills were seen to feed 2,052 times. The proportion of insect food was 36.65% of the total recorded. They are flowers, seeds, buds or picked at the leaves or stems of 40 species of plants. The acacia tree and the six species of understory plants listed above were the most important food plants (the other 33 species constitute only 10.45% of the total observed). Owing to the lack of suitable techniques to sample insect quantity without damaging the habitat, we only monitored the seven major plant foods in 1988-89. We recorded their locations within the study site and tracked their flowering, seeding or fruiting schedule. To quantify the amount of food available to the parrotbills, every other week we counted the number of flower heads, seed stalks or fruit clusters within a quarter area (5 × 5 m) in each quadrat (Fig. 1). An effort was made to sample the representative quarter of each quadrat. For miscanthus or panicum

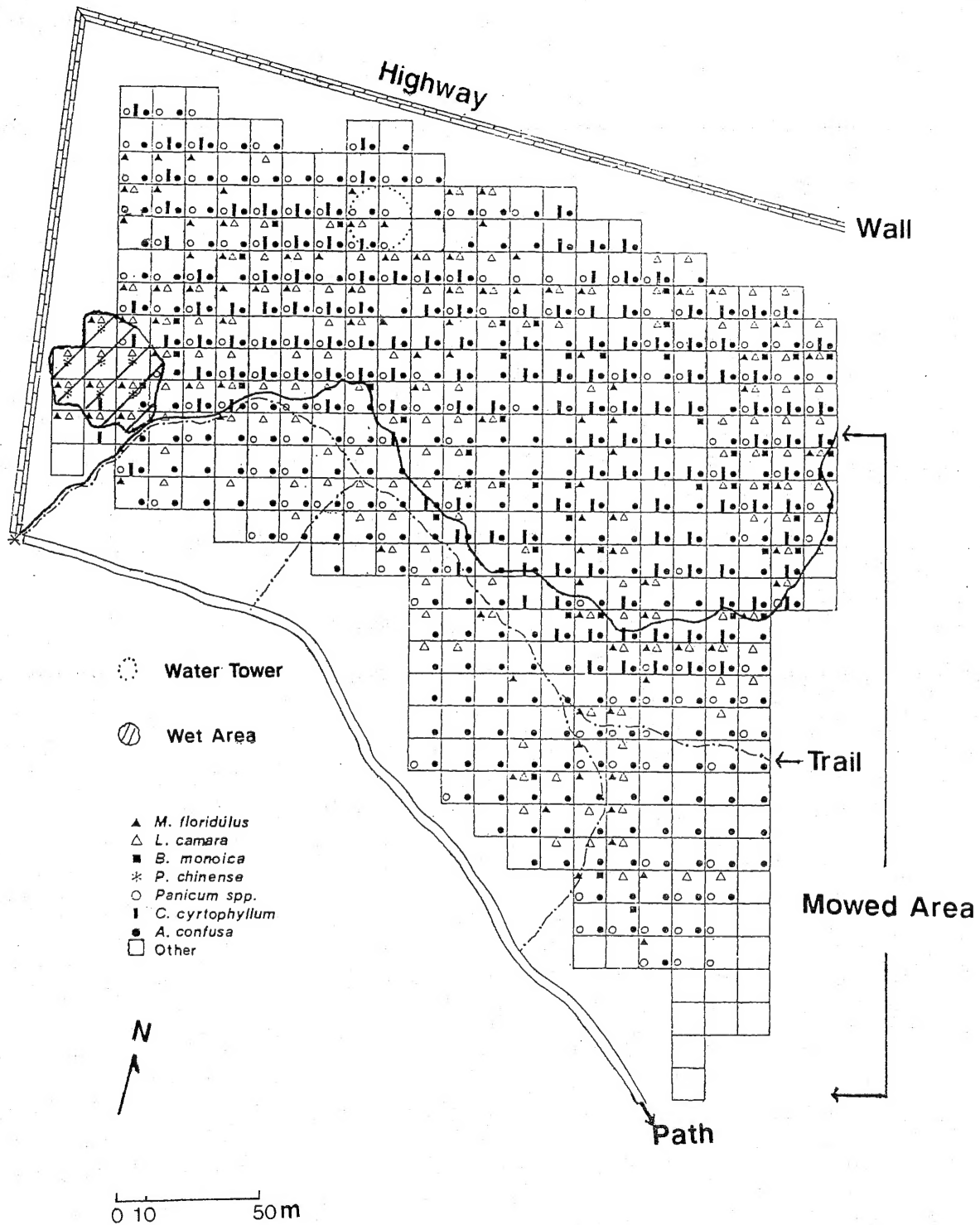


Fig. 1. Map of the 1988-89 study site, showing major landmarks and the distribution of food plants.

grasses, the seed stalks were graded into three classes according to the seed abundance on the stalk, namely full, medium and skimpy.

In the 1988 to 1989 period, we took five samples of the vegetation profile in each 5×5 m area and recorded whether there was vegetation directly above the sampling point at each meter interval. For a given height range, 1 means there was vegetation, while 0 means no vegetation. Thus for each 5×5 m area, the highest total score at each height range could be 5, while the lowest could be zero. For understory shrubs, we took fifteen samples and recorded the internode distance, the angle of the side branches from the main branch, the angle between two side branches, the number of nodes it took for the branching to cover 360 degrees, the diameter of the branch, the number of terminal leaves on a branch, and the mean area of these leaves. We also estimated the total volume of shrubs within each 5×5 m area and took three samples of the branch density (number of branches per cubic meter of shrubs). For grasses such as *M. floridulus* and *Panicum* spp., we measured its total coverage and took five samples of the number of stems touching a 50 cm ruler.

To obtain the distance between adjacent branches that a bird might have to travel when foraging in shrubs, the following equation was used:

$$D = IT^2 + 2IT^2 \sin^2 v (1 - \cos h)$$

in which D is the distance between branches, IT is the internode distance, v is the angle between two side branches, and h the angle between a side branch and the main branch. This equation is based on the assumption that internode distances are the same on the main and side branches on the shrubs.

The total leaf area is the product of mean leaf area, mean number of leaves

on a terminal stem, density of branches and the total volume of the shrubs.

For analyses, we converted flowers and fruits into equivalent units with weights calculated from the frequency they were consumed at in the past five years. For grasses, full seed stalks got a weight of 3, medium a 2, and skimpy a 1.

The amount of time a flock of birds stayed in a grid multiplied with the number of birds present was used as the utilization value for the grid.

For data analysis we used the SAS computer package.

RESULTS

Parrotbills were primarily understory dwellers (Fig. 2). Parrotbill flocks spent large amounts of time in the canopy only when acacias were blooming or bearing seeds. During the winter months when trees were not blooming or seeding, parrotbills spent less than 5% of their time in the canopy. When *Casuarina* spp. bore seeds in February and March in 1984, the proportion of time parrotbills spent in the canopy increased.

They zigzagged through their habitat on foraging trips. Their path was not always linear between food patches, for they often detoured to avoid crossing wide open spaces. Instead they often followed dense vegetation to where the opening was narrow before crossing over to the other patch. On any given day they might return to forage in a previously visited area (Fig. 3).

In the 1983-84 study period, some locations were visited by parrotbills daily, other places were visited after a number of days. We marked off the map of the study area into 40×40 m squares, and grouped the squares into areas visited by parrotbills every 1, 2, 3, 4 and 5 or more days. I compared the degree parrotbills

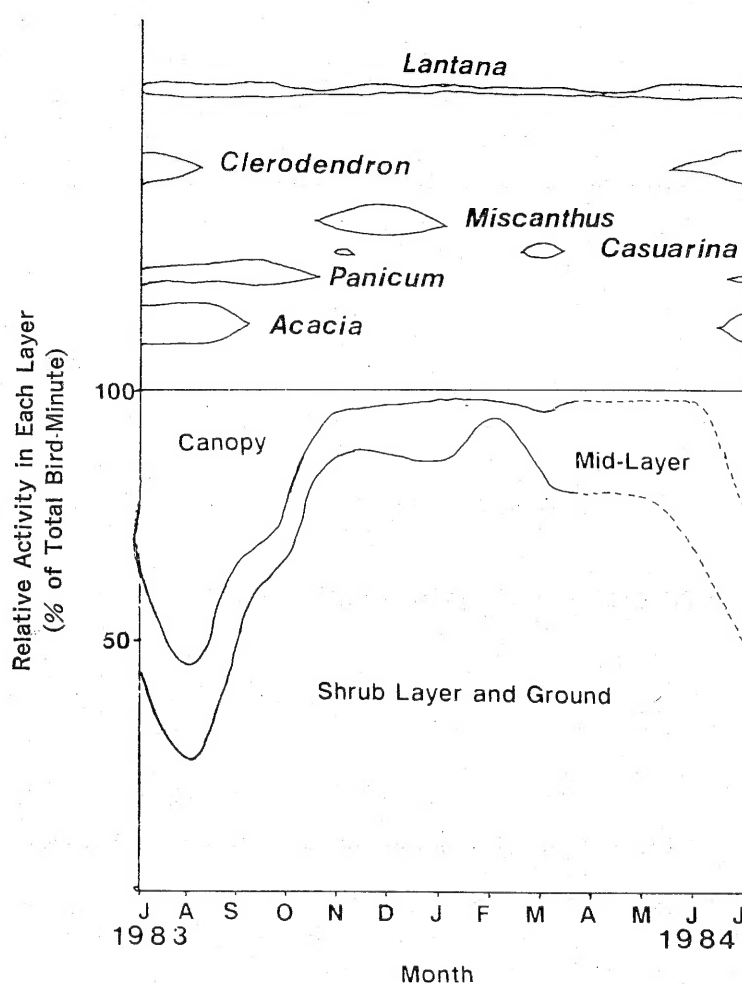


Fig. 2. The activity pattern of parrotbills in the three habitat strata during 1983-84, calculated as relative frequency of occurrence in bird minutes. The upper part of the figure shows the plant foods available for each month. The width of the markings indicate relative abundance.

used the areas in these groups (utilization value, Table 1) with an analysis of variance. The results showed that some areas had a high utilization value but were not visited again within five days. These areas probably had their resources depleted by the bird flock during each visit, and their food replenishing rate was slow. For areas where the bird flocks revisited within five days, there was a significant trend that, on average, areas visited more frequently (with less days between visits) were used more each time than areas used less frequently.

Data from 1988-89 showed the same significant pattern as in 1983-84. Among grids used on the first day, those used again on the second day were used significantly more heavily on the first day than those not used on the second day (Table 2). The utilization values of the two days had a significant positive correlation ($r=0.53$, $p<0.0001$). When the utilization values of the second day were plotted against those of the first day (Fig. 4), it was apparent that grids heavily used on day one were also heavily used on day two. But grids used

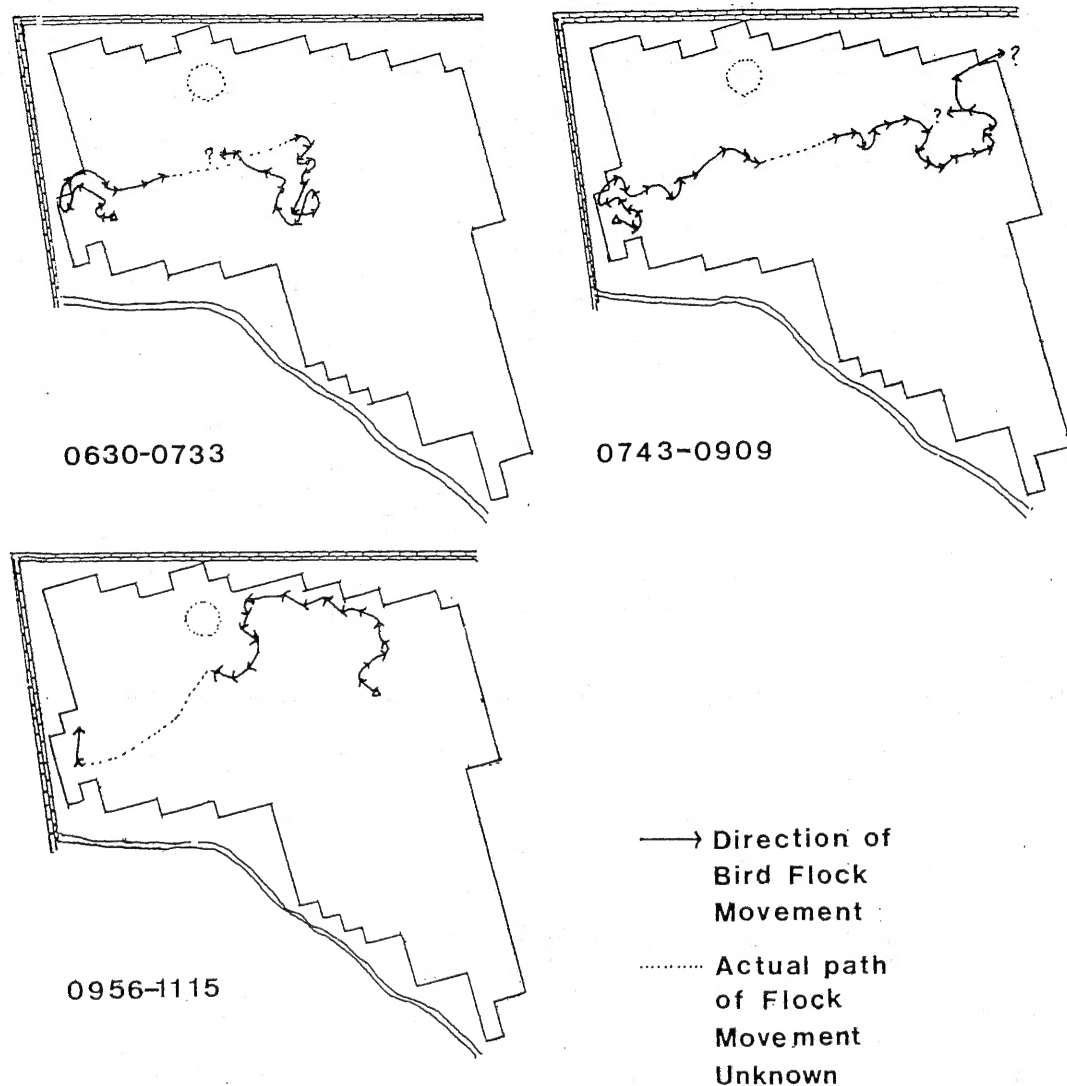


Fig. 3. The foraging path of a flock of parrotbills on 28 Feb. 1990. As shown, this flock of birds zigzagged through their habitat and returned to specific areas in their habitat repeatedly. This pattern suggests the flock of birds was choosing foraging localities, and was sampling a wide region between long stays in specific areas.

lightly or to a medium amount on day one had more variation in the degree of utilization on day two.

The vegetation profiles of the different quadrates were grouped into 50 types through cluster analysis. Some types were common while many types were rare (Fig. 5). The most common types cover the major successional stages from grassy areas to mature broad leaf woods (Fig. 6). The rare types fall into

middle successional stages. No relationship exists between the vegetation-profile cluster type and the amount of plant food available in each quadrate (analysis of variance, $p > 0.5$).

In 1988 and 1989, the grass in 140 quadrates in the study area (385 quadrates in all) was periodically mowed. The parrotbills never visited the mowed areas from November through March. Because the mowed areas were frequently distur-

Table 1
Comparison of resource utilization values between 40 m blocks with
different revisitation rates from Oct. 1983 to Feb. 1984

Day Between Revisits	Mean Utilization Value (No. birds×time spent in block)	Frequency
1	575.7±1291.5	103
2	302.7± 389.2	34
3	227.5± 237.4	5
4	77.4± 35.7	4
5 or more	452.3± 862.4	449

Analysis of Variance of Utilization Values

Sources of variance	D. F.	Sum of Square	Mean Square	F
Groups by days between revisits	4	3103097.9	775774.5	0.90
Error	590	508546927.6	861943.95	
Total	594	511650025.5		

$p < 0.05$

Frequency refers to the total number of times bird flocks returned to a grid the next day, the third day, etc., during field days. Because bird flocks were followed continuously in these days, these numbers were not samples but were what happened during the time period.

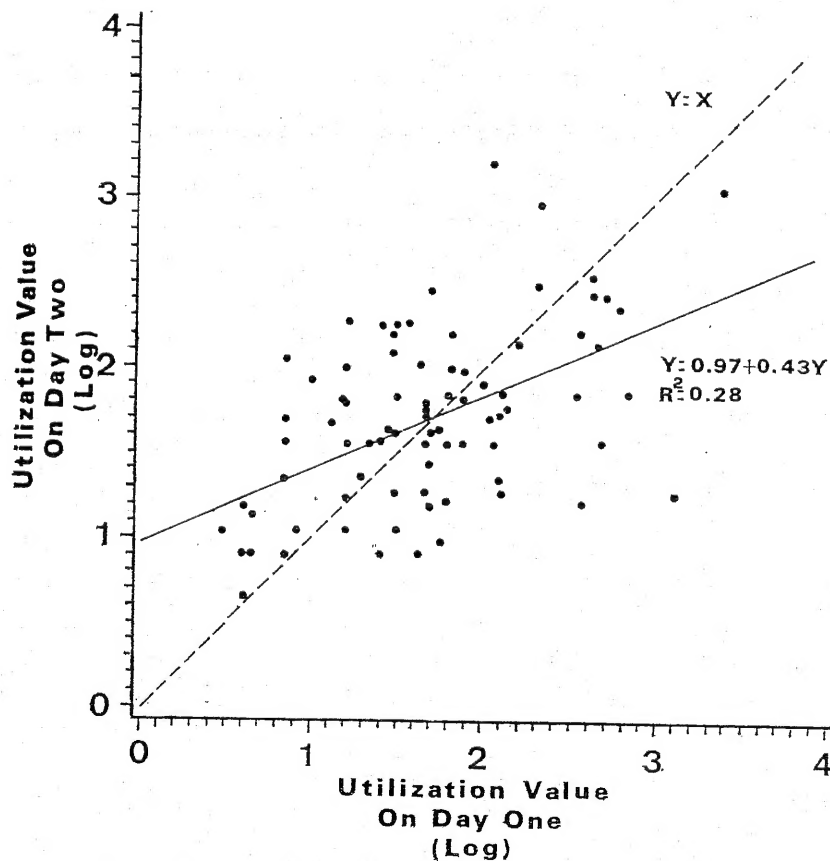


Fig. 4. The relationship in utilization values between grids used on day one and on day two.

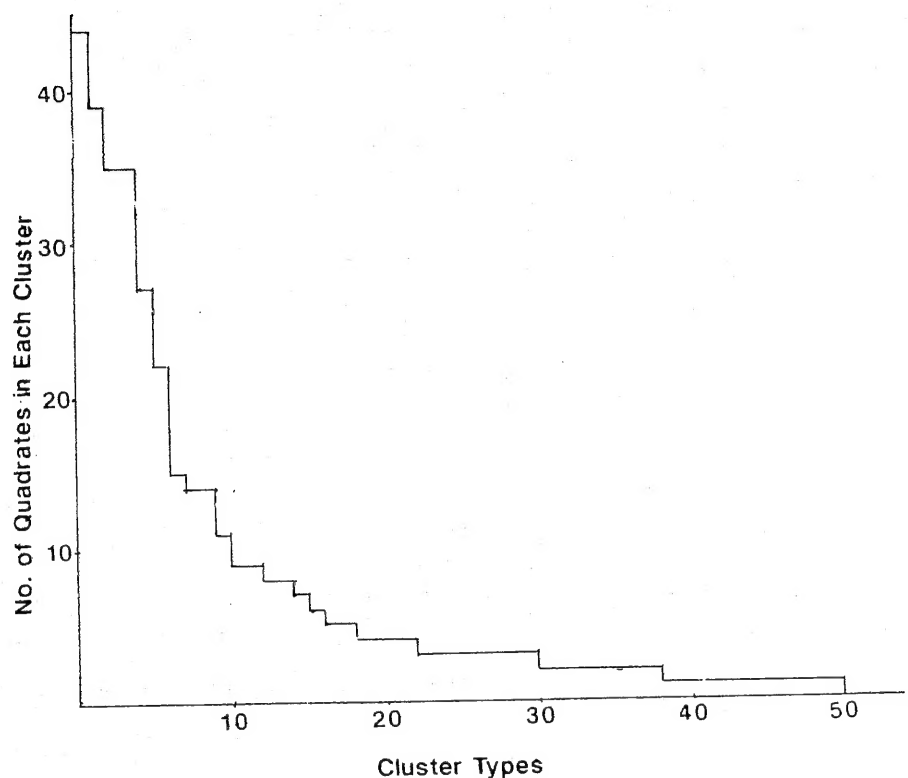


Fig. 5. The frequency distribution of the 50 cluster types of vegetation profiles in the study site of 1988-89.

Table 2

Using only grids visited in day one, a comparison of the utilization values for those visited on day two vs those not visited on day two

Status on Day Two	<i>n</i>	Mean Utilization Value on Day One (Log)	Std	<i>t</i>	<i>df</i>	<i>p</i>
Not visited	99	1.397	0.450	2.952	143.3	0.0037
Visited	83	1.64	40.641			

bed, had few food plants left, and were never used by the birds; they were excluded from the following analyses. As a result, the following analyses were all based on a sample size of 245 quadrates unless noted otherwise.

The undisturbed areas were not used equally by parrotbills. The types of vegetation cluster most intensely used by

parrotbills were primarily quadrates at the early or middle successional stages (Fig. 7). However, not all early to middle successional areas were used. I compared the vegetation profiles of the quadrates where parrotbills visited ($n=197$) and where they never visited ($n=48$) with a discriminant function analysis. The result

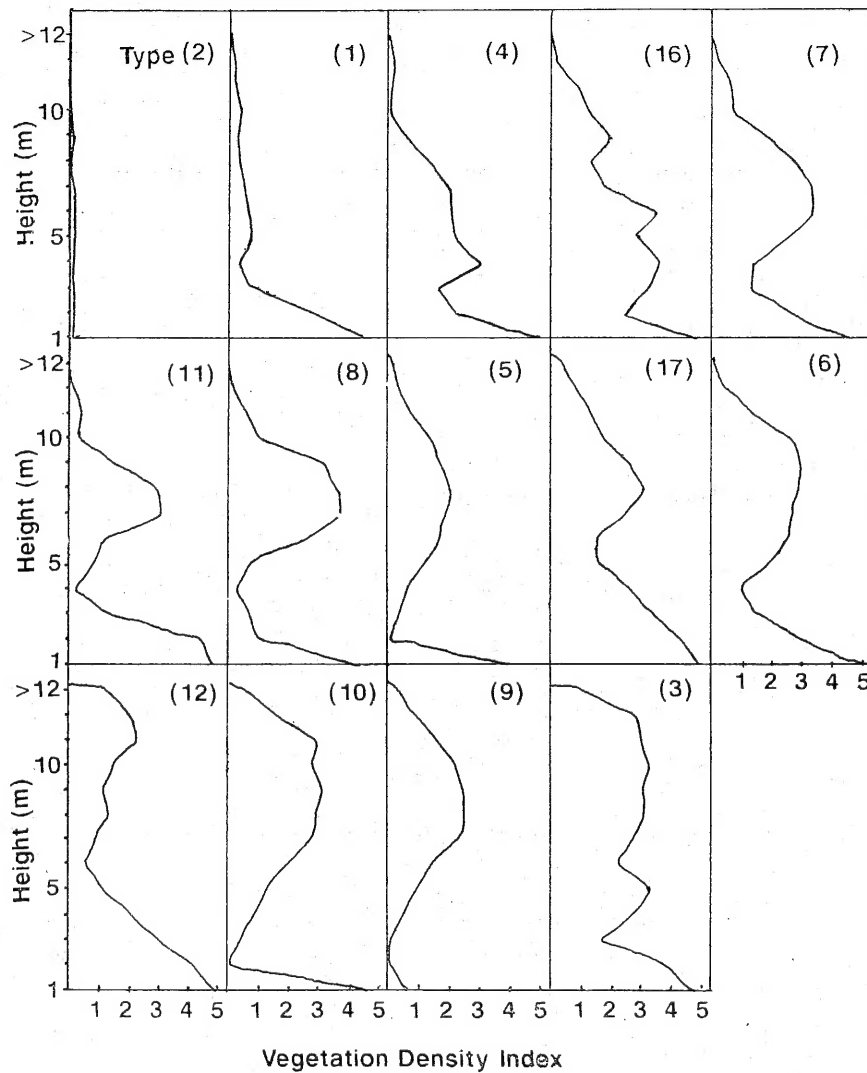


Fig. 6. The vegetation profiles of the 14 most common cluster types.

shows that these two categories cannot be separated by vegetation structure alone. This suggests that vegetation profile was not an important factor influencing the activity patterns of the parrotbill flocks.

Between December 1988 and March 1989, parrotbills used only the ground to shrub and the middle layer of the woods. Because sometimes a few birds would linger to forage in a place while the main flock moved on the parrotbill flock size did not remain the same throughout each day.

To determine whether the flock preferred denser vegetation when the bird flock was smaller, a Pearson's correlation of flock size seen in each quadrat was calculated against the local vegetation density and against vegetation volume. The results show that both have significant but very low correlations with flock size ($r=0.06$ for flock size and volume, $r=0.08$ for flock size and density $p<0.05$). This suggests that where the flock of birds went was not significantly influenced by flock size.

From December through March, par-

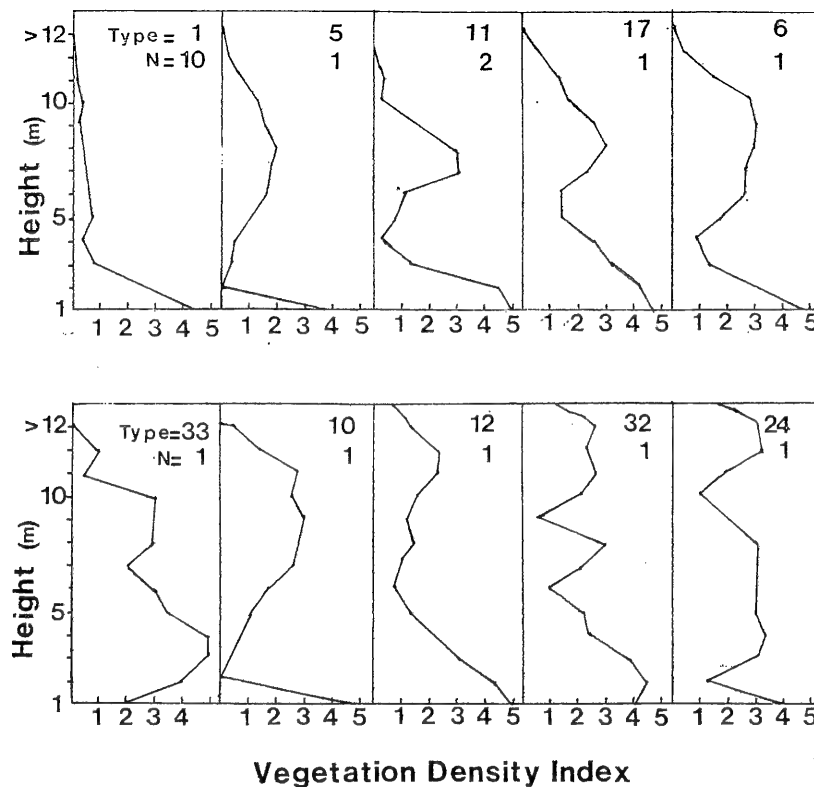


Fig. 7. The vegetation profiles for the cluster types of the 20 most heavily used quadrates. Each of the 10 cluster types had other quadrates used to a lesser degree or even not used.

rotbills used both areas with and without shrubs. The frequency they foraged in grassy or open areas was not significantly

different from what was expected ($\chi^2=0.71$, $df=1$, $p>0.05$, Table 2). Parrotbills preferred foraging in places where the

Table 3
The utilization pattern of open areas in 1988-1989

Distance	Not Used	Infrequently Used	Frequently Used	Total
Open Area	28 (24.4)	59 (62.4)	28 (28.2)	115
Grass and Shrub	24 (27.6)	74 (70.6)	32 (31.8)	130
Total	52	133	60	245

The relative degrees of utilization was determined as follows:

The utilization values of each month was ranked from high to zero. The number of zeros is the number of quadrates not used for that month. The rest of the values were divided as equally as possible into four classes of utilization. Each quadrate was then given a score of 1 to 4 (from low to high values). When considering a specific type of quadrate, such as open areas, the range of mean utilization score of each quadrate was equally divided into two categories: infrequently and frequently used.

Values represent the number of quadrates in each category.

Expected in (). $\chi^2=0.71$, $df=1$, $p>0.05$.

distances between branches were between 6 to 13 cm, especially where the distances were between 6 and 7 cm, but less in areas where the distances between branches were closer ($\chi^2=33.075$, $df=8$, $p<0.005$, Table 4). Because the relationship between branch distances and utilization was not linear, the distance value squared was added as an additional variable for further analyses.

The utilization value for each grid varied from month to month. The utilization values for the different grids in the study site show an exponential distribution every month. A log transformation was performed to normalize the utilization data for further analyses. The locations of the quadrates most frequently visited by parrotbills were concentrated on the western end of the study site (Fig. 8). This region, in addition to having abundant understory plants, also contained a permanently wet area where ground water accumulated. However, no "food" could be identified on the water or mud surface with the naked eye.

Food plants were distributed unevenly in the study site (Fig. 1). Different plant foods became available at different times in different localities. Stepwise regressions were used to detect the relationship

between the degree of habitat utilization and plant food availability in each grid each month (only 5 plant foods were used in this analysis for two species did not flower or seed during the period concerned). The results show that between December and March *L. camara* and *M. floridulus* were the most important species in influencing the habitat use of the parrotbills, but the importance of each species varied from month to month (Table 5). Apparently, a species gained influence when it was the most abundant food source in the habitat (Fig. 9).

There was a positive correlation between the amount of food available and the mean density of stems (Pearson's $r=0.4$, $p=0.0001$), and the total numbers of stems (Pearson's $r=0.33$, $p=0.0001$) in each quadrate. The correlation between interbranch distance and the quantity of food ($r=0.23$), and between interbranch distance and mean stem density ($r=0.29$) were both low but significant ($p<0.01$ in both cases).

A linear multiple regression analysis was employed to determine the contribution of environmental variables to the habitat use of parrotbills. Environmental variables considered include month, total amount of *L. camara* and *M. floridulus* available each month (*LC* and *MF*), mean

Table 4
The relationship between utilization value and inter-branch distances

Distance	Not Used	Infrequently Used	Frequently Used	Total
2-3.9 cm	8 (6.09)	20 (18.8)	5 (8.12)	33
4-4.9	8 (5.72)	19 (17.6)	4 (7.63)	31
5-5.9	5 (6.28)	25 (19.4)	4 (8.37)	34
6-6.9	3 (2.58)	2 (8.0)	9 (3.45)	14
>7	0 (3.32)	8 (10.2)	10 (4.43)	18
Total	24	74	32	130

The definition for infrequently and frequently used is the same as in Table 2. Values represent the number of quadrates for each category. Expected in (). $\chi^2=33.075$, $df=8$, $p<0.005$.

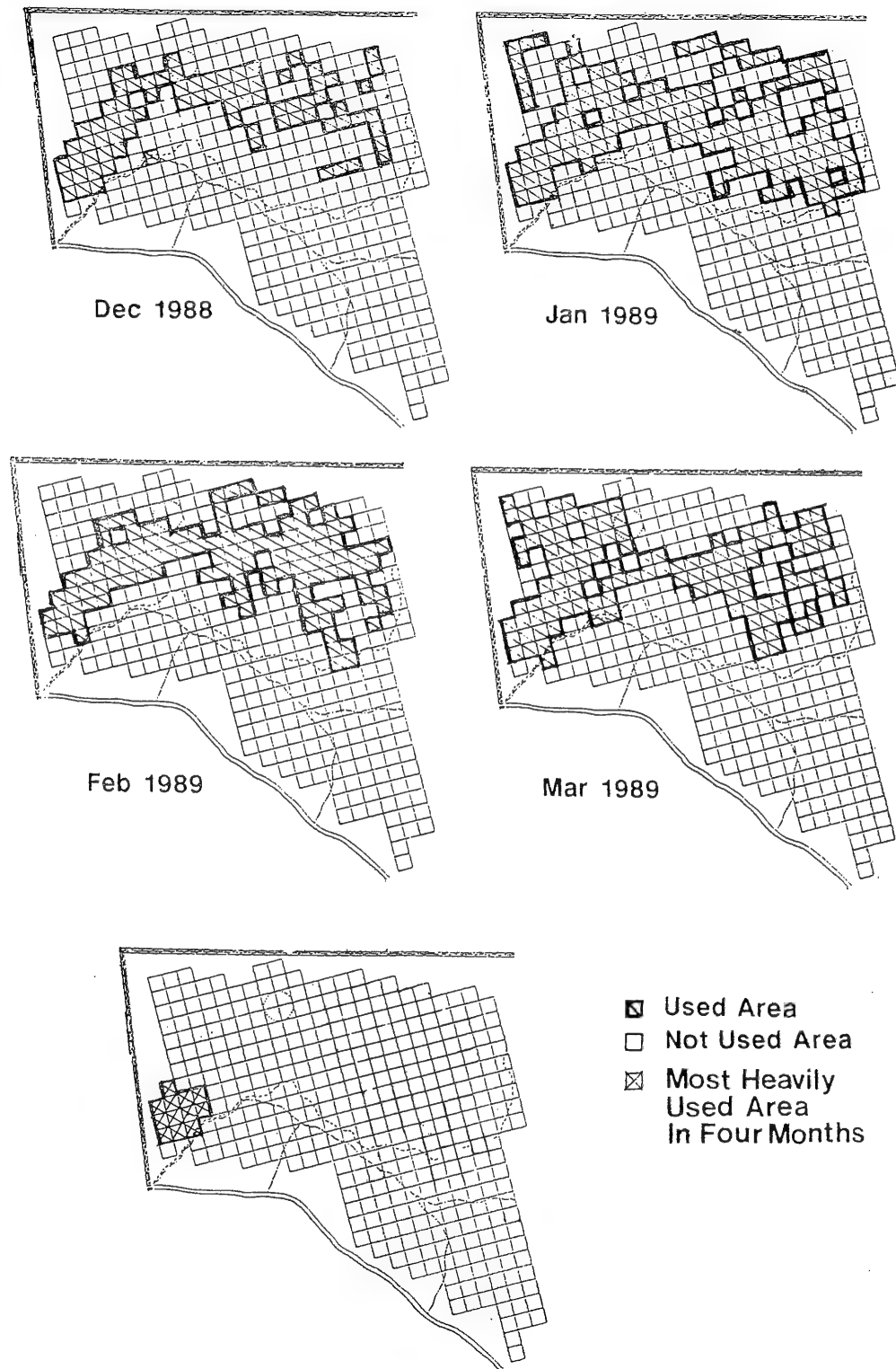


Fig. 8. Areas used by parrotbills each month in the study site of 1988-89. The areas used most heavily during all for months is also shown.

Table 5
A stepwise analysis of the relationship between utilization value
and seven species of major plants

Month	Regression results	R ²
December	Use=1.20+0.0007 <i>L.c.</i> +0.003 <i>M.f.</i>	0.397
January	Use=1.45+0.0009 <i>L.c.</i>	0.27
February	Use=1.39+0.002 <i>L.c.</i> +0.006 <i>M.f.</i>	0.299
March	Use=1.65+0.0014 <i>L.c.</i> +0.015 <i>M.f.</i>	0.418

All relationships significant at $\alpha=0.05$ level.

L.c.=*Lantana camara*

M.f.=*Miscanthus floridulus*

distance between adjacent branches (dist), distance squared, total volume of undergrowth (volume), total number of stems (stem), total number of leaves (leafno), and total leaf area (leafarea). The following equation was obtained:

$$\text{Use} = I_i + a_i LC + b_i MF - 0.028 \text{ dist} + 0.006 \text{ dist}^2 - 0.004 \text{ volume} + 0.0003 \text{ stem} + 0.0000006 \text{ leafno} - 0.00000002 \text{ leafarea}.$$

In this equation, *I* is intercept, *i* is month, while *a* and *b* are the coefficients for *L. camara* and *M. floridulus* each month. Their values are:

<i>i</i>	Intercept	<i>a</i>	<i>b</i>
December	1.999	0.0288	0.0017
January	1.772	0.0286	0.0028
February	1.813	0.0262	0.0010
March	1.548	0.0161	0.0015

The most important variables influencing the habitat use pattern were first the total amount of *LC*, then *MF* available each month in each quadrat ($p=0.0001$ for both). Because of monthly variation in the amount of food available, the equation for different months has different slopes. This variation is also significant ($p=0.0001$). The mean distance between branches and the square of this

value both contributed significantly to the habitat use pattern ($p=0.0011$ and 0.0001 respectively). These were followed by the total number of stems in each quadrat in significance ($p=0.0001$). The contribution of the total volume of undergrowth, the total number of leaves, and the total leaf area in each quadrat were not significant ($p>0.1$). The total amount of variation explained by this model is 0.408.

Using the variables selected in the general linear model above, I checked how well it fitted the reality by using it in a discriminant function analysis. Considering only the grids used on the first day, I asked SAS to score whether each should be re-used on the second day, then compared the results with actual use patterns (Table 6). The parrotbills rarely visited grids that they should avoid, but only visited a portion of the grids they should have visited. The total error count was 28.2%.

The major predators of vinous-throated parrotbills in the study area were feral cats, brown shrikes (*Lanius cristatus*), and snakes. Dense branches form an effective shelter against cats which attack from the ground with paws and shrikes which swoop down from above. I have witnessed parrotbills retreat rapidly into the interior of shrubs upon hearing the

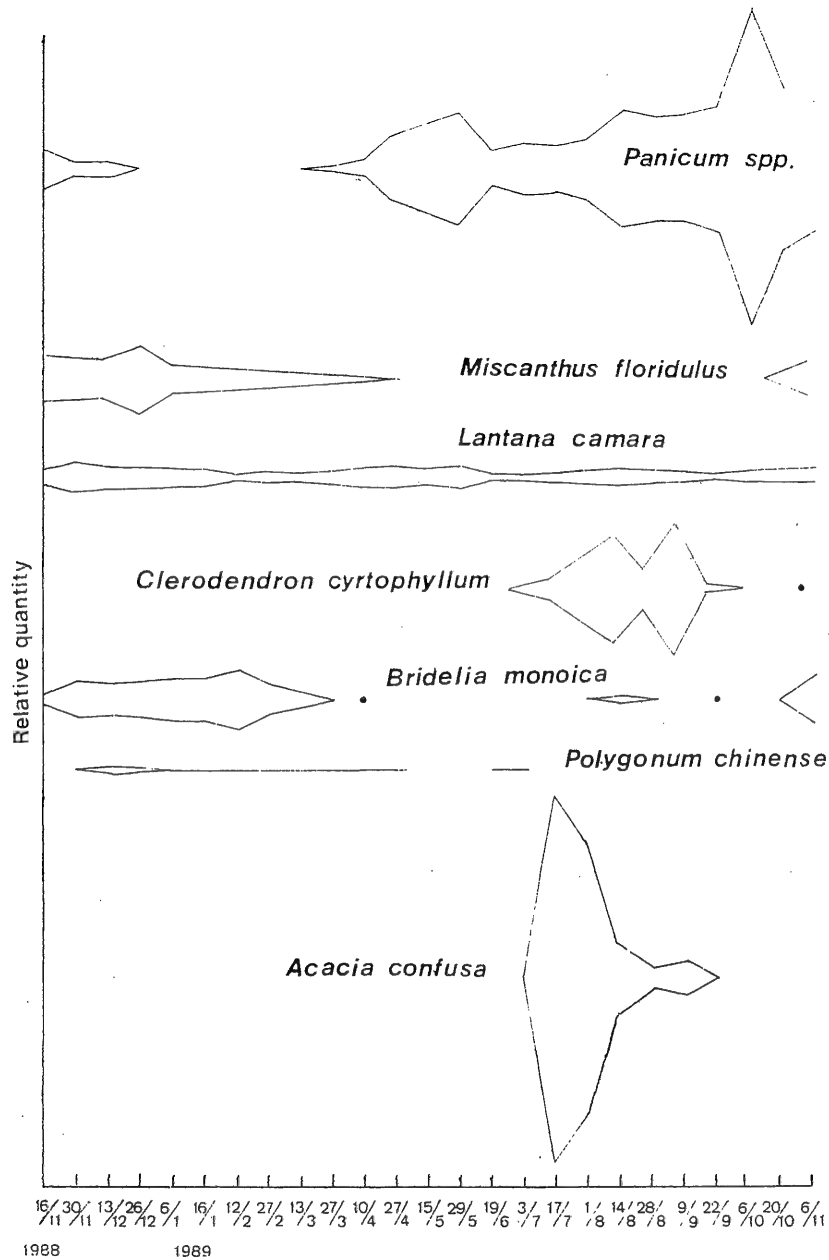


Fig. 9. The relative quantity of the seven major plant foods of parrotbills in 1988-89. The quantities for all except *A. confusa* were on the same scale in the figure, while *A. confusa* was converted to percent of sampling areas covered by seeds or flowers.

sharp alarm call uttered at the approach of a cat or a large swooping shadow. Parrotbills may continue to forage calmly in the interior of dense shrubs as a cat paws at the branches outside. Often a cat or a shrike would give up hunting

attempts after repeated failures. In six years, no free living parrotbill was seen caught by a cat or a shrike. Dense branches provided little protection against snakes, but snakes are primarily predators of nestlings and eggs.

Table 6
Using Discriminant Function to analyze
the usefulness of GLM model

	Should Not Visit	Should Visit
Frequency	99	83
Not visited	92	41
Visited	7	42
Error Count	0.07	0.49
Total Error	0.28	

DISCUSSION

The food patches of vinous-throated parrotbills were unevenly distributed in their habitat. They most likely knew the locations of their food resources, but probably did not know the exact amount of food available in each patch until they got there. The zigzagged foraging routes of parrotbills suggested that they were choosing the next patch as they left the previous one. This foraging pattern is similar to the model suggested by Pyke (1978, 1984).

This study suggests that the most important variable influencing the amount of time a parrotbill flock stays in each locality (utilization value) was the amount of plant food available there. The quantity and quality of plant foods in each locality varied from week to week. Parrotbills apparently were able to monitor this variation and often foraged in good locations. However, their knowledge was not perfect, because there were locations with large amounts of food not visited, while they used some places with no or little plant food. Pyke suggested (1984) that when an animal's knowledge of food distribution in the habitat is not complete, it would spend time sampling different food patches, thus would visit other locations. The facts that parrotbills spent at least a small amount of time in the canopy every month, and they

frequently returned to a particular site visited earlier in the day both support this hypothesis. The parrotbills shift to the canopy when acacia or casuarina bloomed and bore seeds indicates that they kept fairly good track of the quality and quantity of plant foods in their habitat.

Caraco (1979a) suggested that group size should be negatively correlated to the mean quantity of food available in the environment. Pearson (1989) found that the size of a food patch could influence foraging flock size. For social birds in stable flocks, the size of a food patch could influence either the flock size or the duration a flock of birds remain in the patch. Since vinous-throated parrotbill flocks are relatively stable and the few individuals that stayed from a flock usually rejoined it within a few minutes, the influence of food patch size should be expressed primarily in the duration the birds stayed in a food patch. Yet, there was no direct relationship between the quantity of food available and the utilization value of an area, indicating that there were other factors at play.

The second most important variable was the distance between adjacent branches. The relationship between habitat use and distance between branches was not linear, and parrotbills preferred areas with slightly larger distances between adjacent branches. Of course, the difference between these distances was small, the largest distance was only 13 cm. Nevertheless, the preference was very strong. This may have to do with the "gait" size of the parrotbills. When foraging, vinous-throated parrotbills usually hopped from branch to branch, flying only when moving distances too long to hop (Severinghaus, 1987). Vinous-throated parrotbills have a mean body length of 102 mm (std=8, $n=39$) including a 60 mm tail, leg length of 33.5 mm (std=0, $n=2$), and mean

tarsus length 20.1 mm (std=1.4, $n=40$). A distance of 6 to 13 cm, especially 6 to 7 cm, could be covered by an easy hop while distances closer that might be more difficult. Similarly, if flagstones are placed too close together, it would feel awkward and difficult for a person to walk on them and it would actually expend more energy to get through. Parrotbills apparently also made habitat use decisions considering the travelling cost within each type of habitat. Both tracking food abundance and minimizing the travelling cost would maximize an energy return for parrotbills.

Predator avoidance might have also played an important role in parrotbill habitat use pattern because the third most important variable influencing the habitat use of parrotbills was the total number of branches in each grid. In general, areas with dense shrubs or grasses were used more. Flocking birds gain benefits in shared surveillance, improved predator detection, and increased foraging time. Even so, yellow-eyed juncos (Caraco, 1979b) and house sparrows (Grubb and Greenwald, 1982) had to compromise between foraging and predator avoidance needs, by staying close to cover and by-passing the best feeding localities. The results of this study show that vinous-throated parrotbills do not need to compromise between maximizing energy return and predator avoidance. Dense branches similarly gave vinous-throated parrotbills physical protection against predators, but their habitat dense branches or grass stems often supported large amounts of plant food. Dense branches and stems also provided large amounts of substrate for gleaning insects. Thus parrotbills lose little feeding time to predator avoidance by foraging in dense vegetation.

The utilization value of different quadrates were not independent of each other,

because a flock of birds could not arrive at a grid without passing through adjacent ones. Thus, they also travelled through some poorer areas in order to reach preferred places. This unavoidable fact created statistical noise, and explains in part why the r^2 value of the general linear regression model was not higher. Another major shortcoming was our neglect of including insect food in the study. However, we could not easily estimate the quantity of insects in the shrubs and grasses without altering or destroying part of the vegetation, thus influencing the utilization pattern of the bird flock. We also ignored the other 33 species of plants that parrotbills ate or picked at. Possible inaccuracies in field measurements could also lower the r^2 value in our model. Nevertheless, the habitat use pattern of parrotbills was clearly significantly influenced by energetic concern, not only in efficient food intake, but also in energy expenditure, while predation pressure was probably of secondary importance.

According to the discriminant function analysis, this model was successful in separating out grids not suitable for vinous-throated parrotbills to use. The number of poor grids used were very low. So the parrotbills were quite good at avoiding areas no longer "good" for foraging thus could avoid wasting energy. Parrotbills did not maximize their use of "good" grids under this model does not necessarily mean the model is deficient. Perhaps these unused good grids were more isolated, or would have cost more to reach, thus were sacrificed in exchange for overall foraging efficiency.

The significance of energetic concern can explain why parrotbills do not maintain separate territories and use smaller activity areas. Given their small body size, they feed almost continuously. Their food items occur in abundance but where

it is found changes with time. Territory defense takes time away from feeding while it does not increase the amount of food each bird can obtain. To defend a whole season very likely costs more energy than to travel a long distance by hopping. The minimate aggression that parrotbills exhibit gives further support for their need for energy conservation. Caraco (1979a) pointed out that the needs to avoid predation and to search for food put a limit on the time available for aggression. Dominance hierarchy would exist only when it benefits the dominant individuals and when they have time to defend their dominance. Vinous-throated parrotbills show no dominance hierarchy in its flock and almost no aggression. Perhaps they evolved in a feeding-time constrained situation, such as in areas with limited food resources, short days or low temperatures, so they needed to decrease all aggressive interactions. In resource-rich Taiwan, their energy conservation permitted them to expand and adapt to surviving in diverse habitats, resulting in an extremely wide distribution geographically and ecologically.

Acknowledgements: Miss. Su-Hua Chang, Pei-Ling Chen, Li-Yi Cheng, Hsiu-Yun Yen, and Messrs. Shou-Hsien Li, Cheng-Tien Lin and Chia-Hua Li assisted with field data collection. Mss. Chen, Cheng and Mr. S.H. Li spent long hours at computer terminals assisting with data processing. Dr. Lung-An Li of the Institute of Statistics at the Academia Sinica worked out the equation for interbranch distances, and assisted with numerous statistical procedures and interpretations. Dr. Chien-Chung Cheng was a frequent consultant and trouble shooter for computer or statistical problems. This study could not have been completed without their help.

REFERENCES

- Baker, M.C., C.S. Belcher, L.C. Deutsch, G.L. Sherman and D.B. Thompson (1981) Foraging success in junco flocks and the effects of social hierarchy. *Anim. Behav.* **29**: 137-142.
- Berner, T.O. and T.C. Grubb, Jr. (1985) An experimental analysis of mixed-species flocking in birds of deciduous woodland. *Ecology* **66**: 1229-1236.
- Barnard, C.J. (1980) Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). *Anim. Behav.* **28**: 295-309.
- Caraco, T. (1979a) Time budgeting and group size: a theory. *Ecology* **60**: 611-617.
- Caraco, T. (1979b) Time budgeting and group size: a test of theory. *Ecology* **60**: 618-627.
- Caraco, T. (1980) Stochastic dynamics of avian foraging flocks. *Am. Nat.* **115**: 262-275.
- Caraco, T., S. Martindale and H.R. Pulliam (1980) Avian time budgets and distance to cover. *Auk* **97**: 872-875.
- Charnov, E.L. (1976) Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.* **9**: 129-136.
- Cody, M.L. (1971) Finch flocks in the Mohave Desert. *Theor. Popul. Biol.* **2**: 142-158.
- Grubb, T.C. Jr. and L. Greenwald (1982) Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy cost. *Anim. Behav.* **30**: 637-640.
- Krebs, J.R. (1974) Colonial nesting and social feeding as strategies for exploiting food resources in the great blue heron (*Ardea herodias*). *Behaviour* **51**: 99-134.
- Krebs, J.R. (1978) *Optimal foraging: decision rules for predators.* In: Behavioural ecology, an evolutionary approach. Eds. J.R. Krebs and N.B. Davies. Blackwell Scientific Publications. Oxford. pp. 23-63.
- Morse, D.H. (1967) Foraging relationships of brown-headed nuthatches and pine warblers. *Ecology* **48**: 94-103.
- Morse, D.H. (1970) Ecological aspects of some mixed species foraging flocks of birds. *Ecol. Monogr.* **40**: 119-168.
- Norberg, R.A. (1983) Optimal locomotion modes of foraging birds in trees. *Ibis* **125**: 172-180.
- Pearson, S.M. (1989) Food patches and foraging group size in granivorous birds. *Anim. Behav.* **38**: 665-674.

- Powell, G. V. N. (1974) Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Anim. Behav.* **22**: 501-505.
- Pulliam, H. R. (1973) On the advantages of flocking. *J. Theor. Biol.* **38**: 419-422.
- Pyke, G. H. (1978) Optimal foraging: Movement patterns of bumblebees between inflorescences. *Theor. Popul. Biol.* **13**: 72-97.
- Pyke, G. H. (1984) Optimal foraging theory: a critical review. *Ann. Rev. Ecol. Syst.* **15**: 523-575.
- Rubenstein, D. I., R. J. Barnett, R. S. Ridgely and P. H. Klopfer (1977) Adaptive advantages of mixed-species feeding flocks among seed-eating finches in Costa Rica. *Ibis* **119**: 10-21.
- Severinghaus, L. L. (1987) Social behavior of the vinous-throated parrotbill during the non-breeding season. *Bull. Inst. Zool., Academia Sinica* **26**: 231-244.
- Sullivan, K. A. (1984) The advantages of social foraging in downy woodpeckers. *Anim. Behav.* **32**: 16-22.
- Whelan, C. J. (1989) Avian foliage structure preferences for foraging and the effect of prey biomass. *Anim. Behav.* **38**: 839-846.
- Wickler, W. (1985) Coordination of vigilance in bird groups. The "Watchman's Song" hypothesis. *Z. Tierpsychol.* **69**: 250-253.

粉 紅 鸚 嘴 之 棲 地 利 用

劉 小 如

鳥類對棲地利用的情形，可能反應其在覓食、逃避天敵、或其他方面承受的生存壓力，這種現象對成羣活動的鳥也是一樣，鳥羣可能喜歡利用 (1) 資源豐富的地點，(2) 能提供保護或較易逃避天敵的地點，或 (3) 活動時能節省體力的地點。

1983-84 年間，筆者定期追蹤粉紅鸚嘴鳥羣之活動情形，同時記錄棲地中主要植物性食物之種類與數量變化，1988-89 年間，更進一步將 3.85 公頃之棲地標成 10 公尺平方之方格，仔細記錄粉紅鸚嘴鳥羣於其中活動的情形，及主要植物性食物於各方格中之分佈與數量變化，同時也測量各方格中之植被結構。

結果顯示粉紅鸚嘴羣每天均會重複前往某些地區覓食，其他地點則隔一段時間才會重複利用，相隔時間有二、三、四、五或更多天。棲地中絕大部份地區都不會在五天之內被重複利用，但是在會重複利用的地區中，重複得愈快的地區平均每次被利用的程度（鳥羣隻數×停留時間）也愈高，故有些地區是粉紅鸚嘴特別偏好利用的。以多變方統計分析的結果顯示，植物性食物量是影響粉紅鸚嘴利用那個地區及對當地利用程度的最主要因素。粉紅鸚嘴也喜歡灌叢枝條間距在 6-7 公分，可以在枝間輕易跳躍前進的地區，而較少用枝間距更近的地點。由此可見能量的獲得與節約是影響粉紅鸚嘴之棲地利用最重要的考量。除此之外，每方格中之總枝條數也對粉紅鸚嘴之棲地利用有影響。濃密的枝條不但提供保護，也提供較多的位置給昆蟲依附，同時其上往往生長著較多的植物性食物。顯然粉紅鸚嘴不需要為了安全上的顧慮而放棄較好的覓食地點。粉紅鸚嘴可能是在能源受限制的情形下進化而來的。很可能牠在能源節約方面的成功，允許牠成為在臺灣分佈最廣，同時棲域也最廣的一種鳥。

